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THE MATING HABITS OF FOUR SPECIES OF THE BRACHYURA.

F. E. CHIDESTER,

CLARK UNIVERSITY.

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I. INTRODUCTION.

In the course of a study of the general activity of the crayfish which has occupied my attention for the past three years, I became interested in the mating habits of Arthropoda.

During the summer of 1910, while acting as a temporary assistant in the Woods Hole laboratory of the Bureau of Fisheries, I had the opportunity to observe the mating habits of four species of marine crabs, and to experiment with them to determine if possible their manner of sex discrimination.

In this paper I shall briefly describe the results obtained and consider similar work done by various investigators on the other Arthropoda.

Acknowledgment is gratefully made to the Hon. Geo. M. Bowers, U. S. Commissioner of Fisheries, for the opportunity to work in the Woods Hole laboratory; and to Professor J. P. Porter of Clark University for reading and criticising this paper.

2. OBSERVATIONS AND EXPERIMENTS.

The species observed were: *Callinectes hastatus*, the blue crab; *Cancer irroratus*, the common rock crab; *Carcinus mænas*, the green crab; *Platyonychus ocellatus*, the lady crab.

A description of the differences between the male and the female; the virgin female; the ovigerous female and the ovigerous female about to lay, will apply in general for all of the species.

In the male the abdomen is narrow and the intromittent organs or verges are the first pair of abdominal appendages. The paired penes are formed by the everted posterior parts of the efferent ducts. The penes transmit spermatophores down the grooves of the verges into the seminal receptacles of the female.

In the virgin female the abdomen is much like that of the male, except that the telson is narrower. Hay (15) discovered the presence of a pair of hooks which project from the body and fit into a pocket on either side of the abdomen, holding the abdomen tightly flexed against the ventral surface of the carapace. The swimmerets are very small in the virgin female. Crabs moult several times during the summer, according to Herrick (16).

At the moulting the broad abdomen of the ovigerous female is liberated from its narrow quarters in the old virginal shell, and the female is ready for impregnation. The abdomen of the ovigerous female is held flexed only by muscular contraction.

A few days after impregnation, the female may be seen to have two spermatophore plugs projecting slightly from the vaginae and effectually closing the entrance. These plugs are probably secreted by the glands of the male. Andrews has found that the spermatophores of the crayfish are held in the annulus ventralis of the female by plugs secreted by the glands of the male (2). It is not known by me just when the plugs are forced out from the vaginae of the female crab, but probably they are retained until just before the laying. This would be the case if the crabs are to be classed at all with the crayfish in which fertilization is external, and in which the annulus ventralis acts as a *temporary* sperm receptacle.

SPECIMENS STUDIED.

	Males.	Virgin.	Females. Ovigerous.	With Eggs.
Blue crabs.....	3	3		
Rock crabs.....	3	2	7	I
Green crabs.....	2	2	2	
Lady crabs.....	2	2	2	

In the above table the virgin females are those that were brought into the laboratory and moulted there.

Distinction between the ovigerous females showing spermatophore plugs and those not showing them will be made as the experiments are discussed.

The crabs were kept in a sea water aquarium $2 \times 2\frac{1}{2} \times 4$ feet. In the case of the blue crabs, observations and experiments were made only on those confined in this tank. The other species were smaller and individuals were from time to time removed to circular bell jars, 9 in. high and 9 in. in diameter, with about 6 in. of sea water in them.

Blue Crabs.—The female about to moult is seized by a male and carried about by him for a day or two until she is ready to shed her shell. During the pre-moulting period the female is in a normal upright position, being held by the second, third and fourth pair of ambulatory appendages of the male. It is stated by Hay (15) that the male appears able to distinguish the female which is about to moult. I was not able to test this in the blue crabs, but from the observations on the behavior of the rock crabs, green crabs and lady crabs, I am inclined to question the statement and to believe that the male is not able to distinguish the female about to moult except from the fact that she is less resistant. I have noted this sluggishness and apparent weakness in the crayfishes for several days before moulting (7).

When the female is in the process of moulting, she is left for a time by the male. Then he approaches her and turns her over so that her head is beneath his abdomen. I was unable to see the first approaches of the male to the soft-shelled *ovigerous* female, but separated two pairs many times and watched the readjustments.

When the female has been turned so that her ventral surface is apposed to that of the male, and her head is situated beneath his abdomen, both remain quiet for several minutes unless disturbed.

After a period of from thirty seconds to ten minutes, the male taps the female lightly with his first and second ambulatory appendages and turns her slowly around underneath him. The male is not, however, the only active party. No sooner has the female been aroused from her semi-hypnotic state by the movement and tactile stimuli of the male, then she begins to use her ambulatory appendages in turning herself. In order to determine if an external stimulus would cause an early adjustment, I tapped lightly on the edge of the thoracic region of the female, by means of the tip of a small seeker. This was tried on three

successive occasions and in each case the female began to move herself into the copulating position by walking around the legs of the male, placing her legs between and against his. In one of these cases, the female moved so rapidly that the male may have thought she was attempting to escape, for he beat upon her carapace in the attempt to quiet her.

It is extremely interesting to see such activity on the part of the female crab, when one has as a contrast the passivity of the female crayfish.

When the female crab has turned about two thirds of the way around, adjustment of the abdomens must be made. As above stated, the abdomen of the ovigerous female is not bound by hooks to the body and is held flexed by muscular contraction. During the preliminary maneuvers, the abdomen of the female is held slightly extended, and the male must push this partially extended obstacle out still farther and interpose his own telson between it and the body of the female. In the case of the blue crabs this is not difficult. The verges of the male are inserted in the seminal receptacles of the female, and copulation takes place. The male carries the female about, grasping her with the tips of his ambulatory appendages, and holding her for hours, sometimes days. While the act of copulation is going on, the female is exceedingly quiet. The male is very pugnacious. Bachelor males were placed in the vicinity of a mated pair of blue crabs and were beaten away by the vigorous defense of the male in copula.

The two male blue crabs under observation were tested as to their recognition of females, hard and soft, of the three other species. In no case did a male attempt to copulate with an alien female.

Rock Crabs, Green Crabs and Lady Crabs.—These species are all smaller than the blue crabs, and are not materially different in appearance from each other. In the case of the blue crabs, I did not succeed in getting a female with spermatophore plugs. In the case of the three species under present consideration, I did secure several ovigerous females that had been fertilized before they were brought into the laboratory, and also secured a rock crab with eggs.

The method of capture of the female by the male is the same in these crabs as it is in the blue crabs. The ability of the blue crabs to distinguish by sight, however, seems to be greater. In handling the members of the different species, one is struck immediately by the remarkable visual powers of the blue crab. He is alert to moving objects and knows when a body comes within striking distance.

Males of all three species were tested by removing the soft females and replacing them by hard males. They attempted in all cases to copulate with the hard males. Then in the case of the rock crab, two males were tested by placing with them, hard, ovigerous females, in which the spermatophore plugs were not protruding. In these cases, the males succeeded in inserting the verges and actual copulation took place.

In the case of the males with whom were placed other males, the approach of the recently copulating male to the stranger male was made in a similar manner to his approach to the lost partner. When the stranger resisted violently, the other male attempted to beat him into passivity just as he successfully did with the females, hard and soft. Just as I have previously held in the case of the crayfish, I now hold that the ability of the male crab to distinguish the sexes is really a matter of inability to hold and copulate with the male individual. It seems that discrimination is tactual and kinæsthetic.

Among the females captured for me were four ovigerous rock crabs, two ovigerous green crabs and two ovigerous lady crabs, all of which had evidently been fertilized some time before, for they were successfully protected from a second fertilization. For about 3 mm. around the apertures of the seminal receptacles, the shell was soft. In the openings of the vaginae were seen two grayish vermicular plugs. These were pulled out, the operation evidently causing discomfort to the female. The plugs were curved in such a manner that they appeared to have been moulded in the vaginae. At the internal ends were the spermatophores, emptied and flat. In order to determine if these spermatophore plugs were formed before they were visible from the outside, I dissected a female which had been killed two days after copulation, and found that the plugs were present, but that the hardened outer ends were not protruding.

Experiments were made with males of the three species under consideration by placing with them females of the same species known to be fertilized and to have protruding plugs. In no case was a male successful in his attempts to copulate. In the case of one rock crab, the female was beaten into submission and the male succeeded in touching the plugs. The discomfort caused such violent struggles on the part of the female that she was released.

The female rock crab with eggs was placed with a male of the same species, but his efforts to overcome her resistance were futile. In neither the fertilized and spermatophore plug-bearing female, or the egg-bearing female is a true passive state produced by the beating of the chelæ and ambulatory appendages of the male.

In the case of a large male and a small female, the adjustment of the abdomens is very difficult. In the case of one large male it was noted that the adjustment was not possible in the normal position, and that he turned upon his back so that the female floated above him and her abdomen was extended to a greater degree. Then he slowly drew her into position, and having inserted his verges, assumed the normal position above her. In all of the species studied, the female is not passive in the later stages of adjustment, but uses her ambulatory appendages to assist in the turning of her body. I should have liked to place a soft-shelled male with a male that had just been separated from a soft female, but was not able to do so.

3. MATING HABITS OF OTHER ARTHROPODA.

Crustacea.—Herrick did not study the mating habits of the lobster (16) but noted the fact that there were external seminal pouches in the female. He states that the copulation is independent of the moulting of the female. Herrick mentions the discovery by Milne-Edwards of a female *Cancer pagarus* which was fertilized and in which were what Milne-Edwards at first took to be the wands of the male, broken off after copulation as in the insects. Later, Milne-Edwards said in reference to this observation that it seemed probable that the stoppers found in the copulating pouches of the female were "of the nature of spermatophores rather than a fragment of the penis."

Holmes (17) found that in Amphipods the oviposition occurs after the moulting of the female. The males capture the females before the moult and leave them for a few hours, resuming possession of them after the moult. He found that the method of recognition is neither by sight nor smell. He removed antennæ and blackened the eyes, and still the males grasped the females. Holmes concludes that the male has the instinct to seize and carry another individual of the same species, while the female has the instinct to lie quiet when seized. He found that dead individuals were not carried and explained this by the lack of an occasional movement causing a struggle on the part of the male to retain his hold. Holmes has mentioned also the work of Leydig on *Artemia*, in which the latter found that the males of *Artemia* clasp the females by means of peculiarly shaped antennæ, and the two sexes swim about together for several days.

Dohrn (Holmes, 17) noted that the males of copepods while mating, swim about on the backs of the females much as in the Amphipoda.

Dearborn (9), Andrews (2, 3), Chidester (6, 7) and Pearse (26), working with crayfish, have shown that recognition is largely tactual. Andrews discovered the annulus ventralis in *Cambarus*, the American crayfish found east of the Rockies. This serves to retain the spermatophores until the female lays her eggs. In the crayfish, fertilization of the eggs is external. Chidester found (6) that males grasp other males and attempt to copulate with them. Pearse found that males attempt to copulate with dead females of the same and different species (26). Andrews holds that the male recognizes the female as a female because she does not resist, hence the dead or bound male is taken for a female. He says (3): "It is thus possible that from the crayfish standpoint the only difference between the sexes is a difference in behavior and not a difference in form, and moreover a difference received by muscle and touch sense and not in effect upon any other sense organs."

It seems to the writer, that although in the crayfish and the lobster, the males do not capture the females and watch over them while they moult, the process is analogous, for the freshly moulted female is soon captured and fertilized. In the case of

the crayfish which have annuli, the subsequent copulations are futile on account of the presence of the hard vermicular plug deposited in the false pouches by the male. Again, in the lobster and in the European crayfish, *Asacus*, although there are no pouches, the spermatophores would naturally adhere to the freshly moulted surface better than to a surface covered with accretions.

The term "recognition" has been used by Pearse and others without a proper appreciation of the fact that we have absolutely no right to assume a true recognition in the Arthropoda. Andrews has brought out this fact in his statement regarding the crayfish, *Cambarus affinis*. He says (3): "Sex 'recognition' exists apparently, only in the sense that the male may carry out all the stages of conjugation if a female happens to be seized, but not if a male is seized."

"Recognition," it seems to the writer, should be relegated to disuse in speaking of the lower animals. The term "discrimination" may be safely used. Arthropoda may use vision, "contact-odor," kinæsthetic or other senses in *discrimination* without really "recognizing" sex.

Insecta.—Feré, in a study of cockchafers (11) found that sexual coupling failed to take place when the antennæ were removed. He also found that males which had just coupled with females proved sexually attractive to other males. It is not just certain that Feré was correct in supposing that the males were attractive to other males, because the former retained the odor femina. He found similarly in *Bombyx* that males sometimes proved attractive to other males (12).

Mayer, working with moths (21), found that the male moths find the females by smell (Forel's contact odor sense?) rather than by sight. Males flew to the abdomens of females which were placed near the detached winged bodies. Males would pair with a female minus wings, but would not approach a male with female wings. In the moths, there would seem to be a distance-odor perception.

Berlese observed that in flies, there was only a slight activity of the external organs of the male, and a great activity of the female. The male mounted the female, but the female was then

the active party, introducing her ovipositor into the genital atrium of the male (5).

Maeterlinck's popular description of the life of the bee, states that the male honey bee captures the female in her nuptial flight and leaves part of his copulatory appendages in her seminal receptacles (20). The factor of natural selection is active in the mating of the bee, for the strong males are the ones to capture the females.

Fielder (13), Wheeler (34) and others mention the mating of ants. Sex-discrimination is by smell. Forel calls it "contact-odor."

Mitchell (22), worked with mosquitoes, finding that the sexes discriminate each other by the song. The female flies into a cloud of dancing males. It is possible that discrimination is *visual* at first, rather than auditory as Miss Mitchell believes.

In confinement, the female stands quietly on the floor of her cage with the male beneath and clinging with his body parallel to hers. Any disturbance which causes the female to move, when the pair are not copulating, causes the male to seize her again. The mating is repeated every hour or oftener, when the male is excited by a movement of the female. This may be brought about by a tap on the cage. When unconfined, one male unites with several females. A single fertilization lasts for five layings. Miss Mitchell concludes that the male continues to approach the female by means of the olfactory stimuli through the sensitive hairs on the antennæ. Distant localization is according to her idea, by sound; discrimination of the quiescent female near at hand is by smell. Moulting as occurring before fertilization is not mentioned.

Stockard, working with the walking-stick, *Aplopus Mayeri* (32), found that males mated with artificial females made by fastening the abdomens of females to sticks and supporting the sticks on wire legs.

Arachnida.—Montgomery, 1903 (23), and Porter, 1906 (30), have summarized pretty fully the investigation made on the mating habits of spiders. Both these writers have contributed much original investigation. I shall not attempt to give all of the literature, relative to the mating habits of spiders, but content myself with a brief summary of the more important work.

The Peckhams have taken up in detail the courtship of spiders, and hold that (27) in the spiders, Darwin's theory of sexual selection is upheld.

Emerton (10) finds some variation in the ferocity of the female spiders. He states that in *Linyphia* and *Theridion*, the male and female live peaceably together in the same web and the male is not attacked by the female during his approaches.

In *Agalena* the male is the stronger of the two. He takes the female in his mandibles and lays her on one side and inserts one of the palpi; then he turns her so that she lies on the other side with the head in the opposite direction and inserts the other palpus. The female lies as though dead. Emerton holds that the method used in all of the spiders is for the male to discharge the seminal liquor on a little web spun for the purpose, and to dip the palpi in it; then he approaches the female and inserts the palpal organs into her epigynum. One palpal organ at a time is replaced by the other. Emerton believes that few males are eaten by females.

Montgomery has made most extensive studies of the mating habits of spiders (23, 24). He holds that in recognition, touch is the most important and sight is next in importance. He discredits conscious sexual selection on the part of the female.

Porter agrees with Montgomery in his statement that the female chooses that male which "first and most surely announces by his movements that he is a male." Porter found that in the *Argiope* (30) the male waits until the female has moulted, and then successfully mates with her. He found that in some cases the male left the web after approaching the female who was not ready to moult and finding her hostile. After the copulation the female wraps the male just as she does any prey, and leaves him hanging in the web with her old skin. Frequently there are as many as five male spiders on one web.

Petrunkévitch holds that sight is the only sense of sex recognition used in the hunting spiders. After sex has been recognized, courtship begins and touch is the chief means by which the male excites the female and tests her willingness to accept him (29). Petrunkévitch found that, in *Dysdera*, the male approached the female whenever she began to dig.

Nuttall and Merriam have made a study of the copulation of ticks (25). They find that there are three distinct movements in copulation. The male introduces his mouth parts into the sexual orifice of the female, dilating it and probably exciting the female; then he apposes his own sexual aperture to that of the female and expels the spermatophore, whose neck adheres to the tip of his hypostome and is then pushed into the vagina; the next movement on the part of the male is to reintroduce his mouth parts and rupture the tip of the spermatophore.

4. CONCLUSIONS.

1. In the four species of Brachyura studied, sex discrimination is tactual.

2. In the Brachyura, fertilization is effected when the female has recently moulted.

3. Males of the four species studied attempt to mate with males and fertilized females of the same species but do not attempt to mate with individuals of a different species.

4. In the Brachyura, the female is not entirely passive in the movements which precede copulation; she responds to tactual stimuli given by the male.

5. In the Crustacea, as a whole, copulation occurs at any time, regardless of the moulting of the female. It is highly probable that moulting is a necessary condition for successful fertilization.

6. In the Crustacea the female is usually passive during the act of copulation.

7. Sex discrimination in the Crustacea is kinæsthetic and tactual.

8. In the Crustacea, the males generally die soon after fertilization. A small proportion of males live for some time.

9. In the Insecta, sex discrimination is by smell; Forel's "contact-odor sense" is the fully describing term for a large degree of this discrimination.

10. Moulting has not been shown to be a necessary forerunner of fertilization in the Insecta.

11. The males of some species of Insecta die immediately after copulation.

12. In some species of the Arachnida, particularly the spiders, the females devour the males after copulation.

13. Moulting on the part of the female before fertilization is not the rule in spiders. It occurs in some genera.

14. In the ticks, the mouth parts of the male are used to moisten and stimulate the sexual aperture of the female and thus prepare the way for the injection of the spermatophore.

15. Sexual selection on the part of the female has not been definitely established in the Arthropoda. It appears that the successful male is the one who is strong enough or wary enough to mate with the female, or who has learned soonest by his senses the location of the female.

16. Since chance is a great factor in the presence of the male at the proper time, we must consider that the successful male is the one who first demonstrates his maleness to the female. Though strength is a great factor, opportuneness of proximity appears to be a greater one.

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